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The impact of adult diet on parasitoid reproductive performance

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Abstract

Diet is one of the most common influences on parasitoid reproductive traits. The life span, mating ability, fecundity, fertility and sex ratio of parasitoids can be affected by the quality of the adult diet. In the field, parasitoids can rely on different hosts and non-host nutrient sources, such as floral and extra floral nectar, hemipteran honeydew and pollen, and various artificial diets have been used in mass rearing. In addition, some parasitoid species obtain nutrients by feeding on their host while adult (host feeding). In this review, we summarize current knowledge on the impact of the adult diet on reproductive behavior of hymenopteran and dipteran parasitoids, with a particular focus on longevity, offspring production and host searching traits. First, we focus on food preferences and learning abilities of parasitoids to discriminate high quality diets. Second, we analyze the impact of the adult diet on longevity, examining different natural and artificial food sources as well as the effect of their concentration and frequency. Third, we highlight the impact of the adult diet on host foraging. Fourth, we review the impact of adult diet on parasitoid offspring with special reference to (*i*) egg load, maturation and resorption, (*ii*) parasitism, and (*iii*) progeny production and sex ratio. Finally, a number of implications for biological control and Integrated Pest Management are discussed.

Keywords: biological control; Diptera; Hymenoptera; host searching; longevity; offspring production

Key Message

- Here we review current knowledge on the impact of the adult diet on reproductive behavior of hymenopteran and dipteran parasitoids.
- The impact of the adult diet on parasitoid longevity is analyzed, examining different natural food sources, their concentration and frequency, as well as artificial diets currently employed in mass-rearing programs.
- We examine the impact of adult diet on parasitoid offspring, with special reference to egg load, maturation and resorption, parasitism, progeny production and sex ratio.
- Furthermore, we highlight the impact of the adult diet on host searching, then a number of implications for biological control and IPM are discussed.

Author Contribution Statement

GB and GG conceived and designed research. GB, GG, AT, ND, AlC, and AnC selected the literature. GB, GG, AT, ND, AlC and AnC analyzed the data. GB, GG, ND and AT wrote the manuscript.

Introduction

Parasitoids are important organisms in both natural and human-modified environments. In nature, they form important components of ecological food webs and in agriculture they can be used as biological control agents against a number of crop pests of economic importance. Adult female parasitoids have to decide how to allocate their time, mainly dedicated to host or food foraging, to minimize energy waste. Food foraging is usually mediated by the exploitation of visual and olfactory cues, which can cover innately attractive stimuli (Wäckers 1994) as well as learned ones (Giunti et al. 2015). Both play a pivotal role in minimizing costs associated with food searching activities and on adaptation to spatial and temporal variation of food availability (Giunti et al. 2015). Because of their direct implication in biological control programs, parasitoid host-foraging behavior has been widely investigated, but even food-foraging behavior has a key role for biological control since nutrition affects the parasitoid reproductive traits (Jervis and Kidd 1986; Tena et al. 2015).

Previous review papers discussed peculiar aspects of adult parasitoid nutrition, such as the benefits associated to certain food sources (i.e. host feeding reviewed by Jervis and Kidd 1986; floral nectar by Heimpel and Jervis 2005; nectar, pollen and honeydew by Wäckers 2005 and Wäckers et al. 2008), the impact of natural (i.e. flowering species Jervis et al. 1996 and Russell 2005) and artificial (i.e. food spray Wade et al. 2008 and Tena et al. 2015) foods on parasitoid survival in field conditions, as well as the allocation and utilization efficiency of essential nutrients (Jervis et al. 2008). In this review, we summarize current knowledge on the impact of the adult diet on reproductive behavior of hymenopteran and dipteran parasitoids, highlighting the

impact of a broad range of natural and artificial diets on a number of parasitoid life-history traits. In the first section, we focus food searching (mostly preferences and learning abilities of parasitoids). In the second section, we analyze the impact of the adult diet on parasitoid longevity, examining different natural food sources (i.e. plant nectar and pollen, honeydew and host feeding), as well as artificial diets currently employed in mass-rearing programs. In the third section, we highlight the impact of the adult diet on host searching. In the fourth section, we review the impact of adult diet on parasitoid offspring, with special reference to (*i*) egg load, maturation and resorption, (*ii*) fecundity, fertility and parasitism, and (*iii*) sex ratio. Finally, we outline a number of implications for biological control and Integrated Pest Management. Information about dipteran parasitoids are limited and, when available, is presented in a separate paragraph at the end of every section.

The reviewed literature presented here is mainly focused on laboratory studies, whereas field applications are outlined in the conclusion section. In the field, parasitoids can rely on host and non-host nutrient sources, such as floral and extra floral nectar (Lee et al., 2006; Winkler et al. 2006), hemipteran honeydew (Tena et al. 2013a) and pollen (Zhang et al. 2004). Host feeding is not unusual among parasitoids (Jervis and Kidd 1986; Jervis et al. 1996), and at least one species obtains proteins and carbohydrates from host hemolymph (Giron et al. 2002). Moreover, at population level, the host-parasitoid interaction may be altered by parasitoid energetic requirements (Briggs et al. 1995; Evans and England 1996). For this reason, field researchers aim to increase the amount of sugars in the field improving parasitoid efficiency.

In contrast to previous reviews, which have generally focused on a specific food source, here we review the influence of a broad range of nutritional resources on

parasitoid life traits. The nutrients necessary to parasitoid reproduction are partially acquired during the larval stages, and they may be allocated directly to egg production (i.e. proovigenic egg maturation), but also stored as teneral reserves for adult maintenance and reproduction (Jervis et al. 2008). Storage resources may also arise from excess nutrients assimilated during adult nutrition, considering storage a different way to invest resources, comparable to maintenance or reproduction. Nutrients stored in the fat body may be subsequently remobilized through metabolic costs, which are small in comparison to costs associated with egg resorption (Boggs 1992). Overall, insects seem to use carbohydrates as their basic energy resource, while lipids function as long-term energy stores, although in the parasitoid diet the amount of lipid is moderate (Rivero and Casas 1999; Mondy et al. 2006) and most species are unable to synthesize lipids during their adulthood (Ellers 1996; Visser and Ellers 2008).

Food preferences and learning abilities

Among insects, food selection is a common behavior (Waldbauer, 1968). Food sources present in the ecosystem can vary in nutrient composition and diet selectivity is crucial to optimize parasitoid fitness. In nature, adult parasitoids may exploit as sugary sources a broad range of foods, including nectars and honeydew. This latter food source is considered of lower nutritional value (Wäckers et al., 2008); and simulation models indicate that the ability to select for nectar makes parasitoids more efficient under field conditions (Vollhardt et al. 2010). However, honeydew is largely available in agroecosystems and parasitoids' preferences may become adapted to this resource, when they forage in a honeydew-rich microhabitat (Wäckers 2005; Tena et al., 2016). In

137 the case of the parasitoid *Aphytis melinus* DeBach (Hymenoptera: Aphelinidae), which
138 can feed on honeydews excreted by different hemipteran species (Tena et al. 2013a),
139 naïve parasitoids prefer to feed on sugar-rich honeydew than on poor ones (Tena et al.
140 2013b).

141 The preference and selection of artificial sugars by hymenopteran parasitoids
142 have been explored more in detail. *Cotesia glomerata* (L.) (Hymenoptera: Braconidae)
143 feeds on a wide range of natural carbohydrates, but does not accept certain sugars (i.e.
144 galactose, mannose, rhamnose, lactose, raffinose and melibiose at 2 M concentration)
145 when previously provided with water (Wäckers 1999). However, the addition of
146 fructose (1/8 M), but not that of sucrose, increased the response of *C. glomerata*
147 mannose and raffinose (Wäckers 1999), highlighting the effect of food composition on
148 its suitability for parasitoid alimentation. The ichneumonid *Diadegma semiclausum*
149 (Hellén) also exploits trehalose, a peculiar sugar present in hemolymph and in some
150 honeydews, whereas it shows low responses to lactose and melibose (Winkler et al.
151 2005). Moderately stimulatory sugars are also readily accepted by the egg parasitoid
152 *Anaphes iole* Girault (Hymenoptera: Mymaridae) when wasps have been deprived of
153 water and food (Beach et al. 2003).

154 Parasitoids should balance nutrient intake, avoiding toxicity of over-ingestion of
155 plant secondary metabolites or herbivorous digestive excretions and, therefore,
156 experience may alter innate parasitoid preferences, increasing responses for innately
157 unattractive food sources (Kugimiya et al. 2010). Vollhardt et al. (2010) demonstrated
158 that, while naïve *A. ervi* shows no preferences for either flower nectar or honeydew,
159 wasps, which have experienced honeydew nutrition, prefer to feed on nectar. Several
160 studies investigated the ability of parasitoids to learn both non-host (Sato and Takasu

2000; Wäckers et al. 2002; Olson et al. 2003) and host-related olfactory cues (Canale et al. 2014) in association with food reward, altering adult preferences and in-flight orientation.

Impact of the adult diet on parasitoid longevity

The access to appropriate food sources is fundamental for the survival of parasitoids (Idris and Grafius 1995; Jervis et al. 1996; Wyckhuys et al. 2008). Carbohydrate sources as sugar, nectar and honeydew are not always readily available in the agro-ecosystems and this may play a detrimental role in biocontrol programs, since longevity affects directly the impact of parasitoids as biological control agents (Wäckers 2004).

Natural food sources

Nectar and pollen

Plant nectar is an aqueous solution of sugars, amino acids and other compounds, which quantitatively and qualitatively vary among plant species. Generally, the main compounds of nectar are sucrose, glucose and fructose, quickly digestible carbohydrates with high-energy content, equally suitable for parasitoid alimentation (Hogervorst et al. 2007b), which, with few exceptions (Tompkins et al. 2010), can positively influence parasitoid longevity (Jervis et al. 1996). Floral and extra-floral nectars boost adult longevity (Olson and Nechols 1995; Russell 2005). However, flower availability usually

causes a higher increase of longevity in braconid (Olson et al. 2000; Sisterson and Averill 2002; Berndt and Wratten 2005) and mymarid (Cronin and Strong 1990; Jacob et al. 2006; Mutitu et al. 2013) female parasitoids.

The mating status may affect the beneficial effect of nectar on the longevity of female parasitoids. For example, virgin females of *Bathyplectes curculionis* (Thomson) (Hymenoptera: Ichneumonidae) live longer than mated ones when provided with flower nectar of dandelion, phacelia, alfalfa, and even with water alone, whereas no survival effect is recorded when wasps feed on honey solution (Jacob and Evans 2000). Conversely, the mating status does not seem to influence the fitness of male parasitoids fed on nectar. In *Pteromalus cerealellae* (Ashmead) (Hymenoptera: Pteromalidae), food provisioning increases male longevity, irrespective to mating status, while in females, which have longer lifespans respect to males, a negative effect of mating is recorded when nectar is not associated to host-food presence (Onagbola et al. 2007).

The suitability of pollen as food source for parasitoid is narrowly investigated, since is usually considered as less valuable (e.g. for aphid parasitoids see Starý 1969). Females of the trichogrammatid parasitoid *Trichogramma brassicae* Bezdenko (Hymenoptera: Trichogrammatidae) live longer in presence of corn pollen respect to unfed females, although significantly less than those fed with honey or a mixture of honey and corn pollen (Zhang et al. 2004). *Cotesia plutellae* (Kurdjumov) (Hymenoptera: Braconidae) also exploits beebread food (i.e. a mixture of pollen and nectar collected by honeybees), which is rich in proteins, lipids, carbohydrates, enzymes, vitamins and hormone precursors, by prolonging the adult life of both sexes (Soyelu 2013).

209 *Honeydew*

210

211 On contrast to other natural food sources, such as floral and extrafloral nectars,
212 honeydew is primarily a byproduct. Honeydew has not evolved to attract sugar-feeding
213 arthropods and contains plant-derived and aphid synthesized compounds, which can
214 reduce its nutritional suitability (Wäckers et al. 2008). Sugars from hemolymph and
215 honeydew promote *Eretmocerus melanoscutus* and *Encarsia formosa* lifespan, even if
216 *E. formosa* wasps receive no benefits from feeding on trehalose (Hirose et al. 2009), a
217 peculiar carbohydrate of aphid hemolymph present in some honeydews (Hogervorst et
218 al. 2007a). Similar negative responses to trehalose are reported also for *C. glomerata*
219 (Wäckers 2001), *D. semiclausum* (Winkler et al. 2005) and *B. curculionis* (Jacob and
220 Evans 2004), suggesting that insect-produced oligosaccharides are poor food source for
221 parasitoids (Wäckers 2000). Although the sugar profile of honeydew does not always
222 explicate its lower nutritional value, the relatively high viscosity and the tendency of
223 some honeydew sugars to rapidly crystallize could explain its lower suitability
224 compared to nectar (Faria et al. 2008).

225 Despite the general assumption, some honeydews can increase parasitoid
226 longevity as other sugar sources; the ichneumonid *B. curculionis*, as well as the
227 trichogrammatid *Trichogramma ostriniae* Pang and Chen, the pteromalid *Scutellista*
228 *caerulea* (Fonscolombe) and braconid *Psyttalia humilis* (Silvestri) and *Diaeretiella*
229 *rapae* (McIntosh) successfully uses host or non-host honeydew as food source to
230 prolong adult life, with comparable results to honey or nectar nutrition (England and
231 Evans 1997; Fuchsberg et al. 2007; Wang et al. 2011; Varennes et al. 2016). When
232 flower or extra-flower nectars are not available, parasitoids can detect and feed on

233 honeydew from hosts and non-hosts as it has been reported for *A. ervi* (Hogervorst et al.
234 2007a, b) and *A. melinus* (Tena et al. 2013a, b). Even when nectar is available, some
235 parasitoids prefer to feed on honeydew (Lee et al. 2006), which increases adult lifespan
236 less than nectar sources (Lee et al. 2004). Nevertheless, the effects of honeydew on
237 parasitoid longevity greatly depend on the parasitoid species. Dulaurent et al. (2011)
238 investigated the effect of different kind of honeydews on a generalist [*Ooencyrtus*
239 *pityocampae* (Mercet) (Hymenoptera: Encyrtidae)] and a specialist [*Baryscapus*
240 *servadeii* (Domenichini) (Hymenoptera: Eulophidae)] parasitoid. Honeydew feeding
241 had a significant impact on the longevity of the generalist parasitoids, while the
242 specialist species benefited from just specific honeydew types (Dulaurent et al. 2011).
243 Since honeydew-producers directly feed on phloem sap and do not degrade
244 several compounds (Douglas 2003), honeydew reflect phloem sap composition. In this
245 scenario, honeydew may be greatly altered in presence of transgenic plants producing
246 insecticidal proteins. Indeed, *Galanthus nivalis* agglutinin (GNA) ingestion reduces *A.*
247 *ervi* longevity, either when provided directly in a sugar solution or through
248 contaminated honeydew (Hogervorst et al. 2009). Similarly, high concentrations (0.5%
249 w/v) of GNA and concanavalin agglutinin (Con A) significantly reduce the survival
250 chances of *Eulophus pennicornis* (Nees) adult females, altering parasitoid food
251 consumption rates and decreasing food intakes (Wakefield et al. 2010). Moreover, even
252 if generally sap-feeding insects excrete carbohydrates over nitrogen rich nutrients
253 (Wäckers 2000), honeydews with highly concentrated amino acids are not appropriate
254 to prolong lifespan of *Trichogramma* spp. wasps, which can handle their entire life
255 using nitrogen reserves from the larval stages (Ashley and Gonzalez, 1974; McDougall
256 and Mills 1997).

Host feeding

A wide range of parasitoids, estimated at nearly a third of all parasitoids, feed on their host during adulthood (Kidd and Jervis 1991), through both non-destructive (i.e. the host survives after being fed on) and destructive (i.e. the host dies) feeding (Jervis and Kidd 1986). Parasitic wasps host-killing behaviors, over parasitization, comprise also destructive feeding and eventually host stinging. In this context, it is useful to understand how parasitoids decide to exploit the host as food or reproductive resource. Generally, when parasitoid microhabitat includes both sugar-rich foods and hosts, wasps benefit from host feeding coupled with honey (Heimpel et al. 1997; Schmale et al. 2001; Kapranas and Luck 2008) or non-host honeydew (McDougall and Mills 1997), but not from host feeding alone. The exclusive presence of host food may cause divergent effects; while the pteromalid *Dinarmus basalis* Ashmed (Pteromalidae) nearly doubles life expectancy, respect to food-deprived wasps, when only host is provided, no effect is observable on *Heterospilus prosopidis* (Viereck) (Braconidae) and *Anisopteromalus calandrae* (Howard) (Pteromalidae) (Schmale et al. 2001). In contrast, host feeding is fundamental to increase the longevity of the eupelmid parasitoid *Eupelmus vuilletti* (Crawford), mainly due to carbohydrates obtained during host feeding, over lipids and proteins (Giron et al. 2004). Similarly, the presence of host increase adult longevity by itself in *Neochrysocharis formosa* (Westwood) (Hymenoptera: Eulophidae), but the provisioning of honey greater improves wasp lifespan (Liu et al. 2015). Indeed, while non-host food (10% honey solution) increases levels of gut sugar, body sugar and glycogen of *Diglyphus isaea* Walker (Hymenoptera:

281 Eulophidae) females, host-feeding is related to higher levels of lipids, suggesting the
282 essential connection of this kind of feeding to lipid assimilation (Zhang et al. 2011).
283
284 ***Artificial diets***
285
286 Artificial diet suitability has been widely investigated to select food supplements
287 in the field or in the mass rearing. The encyrtid parasitoid *Ooencyrtus nezarae* Ishii
288 naturally uses different kind of food sources, as floral and extra-floral nectars and
289 honeydews (Teraoka and Numata 2000). However, when female wasps are fed
290 continuously with a single food source during autumn, none of them overwinter
291 (Teraoka and Numata 2000). Various artificial diets were proposed to improve
292 longevity, but, even if honey, glucose, galactose and sucrose were profitable supplies for
293 wasps, none of the artificial diets had greater impact respect to natural foods (Teraoka
294 and Numata 2000). Furthermore, Bautista et al. (2001) also investigated the
295 consequence of honey, maple syrup, molasses, sugar cane and ripe coffee on *Fopius*
296 *arisanus* (Sonan) (Hymenoptera: Braconidae) adult longevity, highlighting the
297 unsuitability of sugar cane to prolong parasitoid life (Bautista et al. 2001). On the other
298 hand, Zamek et al. (2013) found that sugar cane diets prolong adult life of
299 *Diachasmimorpha tryoni* females (Cameron) (Hymenoptera: Braconidae) 50% more
300 than honey and golden syrup.
301 Honey is presumably the most studied artificial diet for parasitoid, since it is
302 palatable and cheap. Provision of honey solutions boost mymarid and trichogrammatid
303 parasitoid longevity similarly to flower and extra-flower nectars and even more than
304 honeydew (Irvin et al. 2007; Tunçbilek et al. 2012). Good examples of parasitoid

305 species which impressively benefit of artificial diet are the ectoparasitoid *Mastrus*
306 *ridibundus* (Gravenhorst) (Hymenoptera: Ichneumonidae) and the endoparasitoids
307 *Trichogramma carverae* Oatman and Pinto and *T. brassicae*, which respectively respond
308 to honey diet decupling (Bezemer et al. 2005) or doubling their life expectancy (Gurr
309 and Nicol 2000). Overall, honey solution, as well as dried grape extract, which present
310 high sugar and low protein content, are able to greatly prolong life of the encyrtid
311 parasitoid *Acerophagus papayae* Noyes and Schauff (Divya et al. 2011). Indeed, the
312 addition of protein yeast hydrolysate to sugary sources acts as feed-deterrent and is
313 toxic to *F. arisanus* wasps (Bautista et al. 2001). Also the hyperparasitoids *Lysibia nana*
314 Gravenhorst and *Gelis agilis* Fabricius (Hymenoptera: Ichneumonidae, Cryptinae)
315 benefit from honey diet over a mimic honey composed of pure saccharides (Harvey et
316 al. 2012). The latter result suggests that the amino acids and vitamins present on the
317 honey, as well as other components, are also responsible of its positive effect on
318 parasitoid longevity. Furthermore, no differences on longevity between male and
319 female, as well as between virgin and mated wasps, are recorded for the braconids *C.*
320 *plutellae* and *Phanerotoma franklini* Gahan when fed on artificial solution of sucrose
321 (20%) or honey (50%), suggesting that these two diets have similar nutritional value
322 and that food may quickly replace the energy spent for reproduction (Sisterson and
323 Averill 2002; Mitsunaga et al. 2004).
324 On contrast to the majority of parasitic wasp species, honey provisioning does
325 not alter longevity of the aphelinid parasitoids *E. melanoscutus* and *E. formosa*. The
326 adult life of these hymenopterans ranges from 1 to 7 days, and presumably the energy
327 intake at the emergence is of pivotal importance for the longevity of these wasps (Zang
328 and Liu 2010).

Fruit exudates can be also exploited as food sources by parasitoids. Sivinski et al. (2006) noticed that adult *Diachasmimorpha longicaudata* (Ashmead) (Hymenoptera: Braconidae) can exploit diets of fruit juice or fruit pulp (e.g. orange or peach), with comparable lifespans to those achieved on honey diet. In contrast, simple guava juice administration reduces longevity, by a decreasing of total sugars and glycogen levels, both for *D. longicaudata* and for the figitid *Aganaspis pelleranoi* (Brèthes) (Narváez et al. 2012).

Sugar composition of artificial diet can deeply influence adult parasitoid longevity. Özalp and Emre (2001) investigated the effect of 23 carbohydrates, including mono-, di-, tri- and polysaccharides, on the survival of the parasitoid *Pimpla turionellae* L. (Hymenoptera: Ichneumonidae). The best results were achieved with sucrose diet while some pure monosaccharides (e.g. fructose and galactose) showed detrimental effects (Özalp and Emre 2001). Similarly, the ichneumonid *D. semiclausum* exploits sucrose, maltose, glucose and melibose, while raffinose, lactose and melezitose have no effect on adult longevity (Winkler et al. 2005). Conversely, the egg parasitoid *A. iole* is able to exploit a broad range of sugars, including those from nectar and honeydew, and it shows the higher acceptance rate for the homopteran honeydew sugar trehalulose, with comparable results to sucrose and maltose (Williams and Roane 2007). However, *A. iole* survival is generally greater when provisioned with a mixture of the major nectar sugars (sucrose, glucose, and fructose) than with other suitable saccharides (Williams and Roane 2007).

Many parasitoids do not accumulate lipids as adults and do not replenish lipid levels after emergence from their host (Olson et al. 2000; Giron and Casas 2003; Visser et al. 2010). However, addition of lipids (i.e. olive oil) in the diet increases *C. glomerata*

353 female lipid levels, but the survival is negatively affected in both males and females in
354 presence of olive oil, whose toxicity increases with concentration (Visser and Ellers
355 2012).

356 Similarly to hymenopteran parasitoids, also dipteran ones can improve their life
357 expectancy in response to an appropriate adult nutrition. *Trichopoda giacomellii*
358 (Blanchard) (Diptera: Tachinidae) increases its longevity of over three times when
359 raisins are added to a water-only diet (Coombs 1997). Furthermore, Chen et al. (2005)
360 investigated longevity variations in male and female of *Pseudacteon tricuspis*
361 (Borgmeier) (Diptera: Phoridae) according to exposure to sugar source and temperature.
362 Both males and females lived longer when fed on sugar sources than when sugar-
363 starved, irrespective of temperature (Chen et al. 2005).

364

365 ***Effect of food concentration and frequency***

366

367 Concentration and availability of the food sources in nature vary greatly
368 depending on biotic factors and environmental conditions (Corbet et al. 1979). Usually,
369 life span of sugar fed parasitoids increases with sugar concentration up to a limit
370 (Azzouz et al. 2004; Ellers et al. 2011). In a laboratory assay with five concentrations
371 from 0 to 70% (w/v) solution of glucose-fructose (1:1), *A. ervi* reached the maximum
372 longevity when males and females feed on a 70%. The parasitoid wasps *Asobara tabida*
373 Förster (Hymenoptera: Braconidae) and *Trichopria drosophilae* Perkins (Hymenoptera:
374 Diapriidae) consume the same intake of differentially concentrated sucrose solutions,
375 but they display detrimental effects when provided with a 100% dilution (w/v), while
376 the higher longevity has been recorded for the 80% sucrose solution. Presumably, wasps

377 do not differentiate intake on the basis of the amount of calories consumed, but just on
378 the volume of their stomach, leading to negative effect when ingesting high-
379 concentrated foods (Ellers et al. 2011). The ectoparasitoid *Catolaccus grandis* (Burks)
380 (Hymenoptera: Pteromalidae) also benefits of low-concentrated sugar solution
381 (Morales-Ramos et al. 1996). The viscosity of highly concentrated sugar solutions may
382 also affect the ingestion facility of parasitoids. Intermediate concentrations revealed to
383 greater contribute to *P. lounsburyi* longevity (Williams et al. 2015), increasing the time
384 spent searching for hosts and reducing resting and feeding periods, when wasps are
385 more subjected to predator attacks (Völkl and Kroupa 1997; Lightle et al. 2010).
386 The value of a single meal can be crucial for survival when sources are spatially
387 or temporally scarce. Different concentrations of *Brassica* flower nectar act
388 differentially on the braconid *C. rubecula* when a single honey meal is offered, with
389 greater benefits when sugar concentration is just below 50% (Siekmann et al. 2001).
390 Timing and sugar concentration of a single feeding activity may also influence *Psyttalia*
391 *lounsburyi* (Silvestri) (Hymenoptera: Braconidae) longevity, increasing the survival
392 chances from 32.3% to 95.4% compared to water control after 2 days (Williams et al.
393 2015). Furthermore, parasitoids exposed to longer food-deprivation periods show
394 longest feeding durations, and thus major energy intakes (Williams et al. 2015).
395 Feeding frequency is crucial for parasitoid survivorship. Overall, daily food
396 provisioning produces major longevity benefits, respect to longer feeding intervals (Lee
397 and Heimpel 2008a). For example, *T. platneri* wasps prefer honey or sugars daily
398 nutrition supplies respect to longer feeding intervals, mainly to overcome the
399 evaporation of sugar solutions. However, the addition of stabilizing agents does not
400 reduce evaporation nor enhance adult longevity (McDougall and Mills 1997). In this

401 scenario, it is raising the hypothesis that dietary restriction, in absence of strong
402 malnutrition, may prolong invertebrates' life (Ellers et al. 2011). Proovigenic parasitoid
403 species, which emerge with an egg-load ready for oviposition (Jervis et al. 2001) and
404 which present a relatively simple diet, mainly or exclusively constituted by
405 carbohydrates (Wäckers 2001), can exploit dietary restriction. For *Macrocentrus*
406 *grandii* (Goidanich) a constant supply of sugars is not necessary to achieve the
407 maximum survivorship (Fadamiro and Heimpel 2001). Indeed, the maximum level of
408 gut sugars is obtained after a single day of food provisioning and decreases substantially
409 one day post-feeding, suggesting that, during starvation intervals, gut sugars are
410 mobilized to maintain constant the level of parasitoid body sugars (Fadamiro and
411 Heimpel 2001). Nevertheless, no beneficial effect of caloric restriction in the
412 intermittent feeding has been recorded so far, since *ad libitum* and daily provisioning of
413 food positively influence the wasps' lifespan (Azzouz et al. 2004; Wu et al. 2008; Ellers
414 et al. 2011). As infrequent feeding opportunities seem to have limited benefits, the
415 habitat manipulation and the mass rearing programs should provide a continuous supply
416 of sugar or nectars to parasitoids.
417
418
419 **Impact of the diet on host searching**
420
421 Host searching is a key behavior, which should be efficient and reduce the
422 parasitoid exposure time to predation. Indeed, for parasitic wasps, food and host sources
423 are often spatially distant. Whereas, host feeding and host honeydew are strictly
424 dependent on host presence, many other suitable food sources, as plant nectars and non-

host honeydew, are not always associated with host and parasitic wasps need to move between different microhabitats during their foraging activities.

Nutrition may positively alter parasitoid physiology, reflecting on responsiveness to different olfactory sources and orientation toward the host, but likely up to a limit. For example, the endoparasitoid *Apanteles aristoteliae* Viereck (Hymenoptera: Braconidae) increases its nutritional state when feeds on sugar-rich sources. However, females with the highest levels of sugars are less prone to make a choice in olfactometer bioassays, while wasps with intermediate level are more expected to orient toward the host (Lightle et al. 2010). In other species, on contrast, females do not profit from nutrition, since starvation does not decrease searching ability (Gomez et al. 2012), usually preferring host cues to food (Pietrantuono et al. 2012).

High abundance of rich food sources is typically associated with an increasing of searching ability respect to the absence of nutrient supply (Takasu and Hirose 1991). Indeed, food provisioning could reduce time spent to locate and accept the hosts, by increasing parasitoid mobility and sensitivity to olfactory cues, but also host acceptance itself (Sisterson and Averill 2002). The frequency of food administration plays a pivotal role on olfactory orientation in parasitic wasps. In wind tunnel assays, female wasps modify their preferences toward host- and flower-associated odors in relation to their feeding status. While well-fed wasps prefer host stimuli, host and food stimuli seem equally attractive for hungry females, which employ more time to start searching behavior and to locate a cue (Jacob and Evans 2001, Siekmann et al. 2004).

Among parasitic wasps, flight ability is generally related to the presence of peculiar diet components, which may alter parasitoid in-flight orientation. The main fuel source employed for flight seems to be glycogen. Indeed, *Venturia canescens* (Grav.)

(Hymenoptera: Ichneumonidae) wasps decreased their glycogen content during flight, and females consume about the 50% of their glycogen storage in one hour of active flight, while glucose, protein and lipid remain constant (Amat et al. 2012). Furthermore, an arrhenotokous strain, which flies more frequently between host and food, has a higher glycogen load at emergence compared to thelytokous strain, reflecting also on a higher flight speed (Amat et al. 2012). Wanner et al. (2006) reported that *C. glomerata* females showed different flight ability according to source type, whereas no differences were noted for males. Furthermore, *ad libitum* feeding on *Anethum graveolens*, as well as on honey solution, increases the total distance flown, the number and the duration of flights completed by female parasitoids. Conversely, other diets have lower or none effects on parasitoid flight behavior (Wanner et al. 2006). Contrasting findings were instead reported for proovigenic species. Indeed, while synovigenic wasps need food provisioning for both somatic and reproductive functions, nutrition has a moderate impact on proovigenic females, which could not benefit from food supply and could eventually rely on their larval energy storage to respond to maintenance and locomotion (Fischbein et al. 2011).

In field condition, the interaction between nutritional state of parasitoids and the presence of food sources may influence the foraging behavior of females. In small corn and soybean plots without food sources, well-fed *Microplitis croceipes* (Cresson) (Hymenoptera: Braconidae) wasps spend more time for host searching and parasitize a higher number of host rather than unfed ones (Takasu and Lewis 1995). However, when supplemental food sources are provided, unfed females are more ready to feed on it and start immediately to search and parasitize hosts (Takasu and Lewis 1995). Similarly, in citrus groves, Tena et al. (2015) found that *A. melinus* females lay more eggs in trees

where artificial sugars are provided than in control ones, suggesting an increase of searching ability.

Impact of adult diet on parasitoid offspring

It is acknowledged that carbohydrate rich diets enhance the lifespan fecundity of parasitoids under laboratory condition (Jervis et al. 1996; Wäckers 2005), while lipids and proteins, either from diet and teneral reserves, are usually necessary for successful productions of the eggs (Ellers and van Alphen 1997). Furthermore, egg hatching and parasitization ability are also processes depending on nutritional status of female parasitoids, and the balanced acquisition of nutrients has great influence also on the size and the number of egg produced (Wheeler 1996; Harvey et al. 2012).

Egg load, maturation and resorption

Egg maturation in female parasitoids is considered a fitness-related parameter, which may influence the reproductive potential of biological control agents and thus population dynamics of hosts. However, different diets may affect the lifetime egg maturation patterns of synovigenic parasitoid species, whose females emerge with no or few mature oocytes, maturing the remaining eggs throughout their adult life. In contrast, for proovigneic species, whose females emerge with their set of eggs completely mature, the effect of diet is almost insignificant (Jervis et al. 2001). The effect of sugar-rich diet on lifetime egg maturation patterns of synovigenic species, both in presence or absence of host prey, has been widely investigated. Typically, parasitoid egg load

497 depends on the diet provided to adult females, as reported for the parasitoid *P.*
498 *cerealellae* (Onagbola et al. 2007). Honey is usually the most effective sugar source to
499 promote egg maturation (Hogervorst et al. 2007a; Hopkinson et al. 2013), and when it is
500 replaced with sugar-poor diets, ovaries of gravid *F. arisanus* females show deterioration,
501 by decreasing egg load from over 100 eggs to less than 70 immediately before their
502 death (Bautista et al. 2001). The maximum egg load of the ichneumonid parasitoid *B.*
503 *curculionis* greater benefits from honey (+15%) than from honeydew excreted by the
504 pea aphid, *Acyrthosiphon pisum* (Harris) (England and Evans 1997). Nevertheless,
505 distinct parasitoid species can differently benefit from artificial diets, as noted for
506 hymenopteran parasitoids of tephritids. Thus, although the egg load of *D. longicaudata*
507 is not altered by diet, *A. pelleranoi* has higher egg loads when fed on honey or pollen
508 than on juice (Narváez et al. 2012). Similarly, egg production is improved by various
509 pure carbohydrates solutions in *P. turionellae*, whereas galactose and trehalose have a
510 detrimental effect (Özalp and Emre 2001). Apart from the intrinsic quality of food, its
511 availability over time can also affect fitness-related traits and may alter egg maturation.
512 Ellers et al. (2011) investigated the effect of dietary restriction (i.e. diet dilution and
513 intermittent feeding) on *A. tabida* and *T. drosophilae*, nonetheless no effect of dietary
514 regime is recorded on fecundity of both species.
515 Parasitoids feeding with diets lacking in sugars generally have to accept
516 compromises, and thus to relocate energy, to mature eggs. For example, starved *Mastrus*
517 *ridibundus* (Gravenhorst) (Hymenoptera: Ichneumonidae) wasps reduce their
518 reproductive potential by decreasing egg size and maturation, as well as the number of
519 attacked host (Bezemer et al. 2005). To economize energy for egg maturation,
520 parasitoids can produce smaller and nutrient poor eggs, can use reserve energy obtained

521 during immature development, and can minimize energy employed for other activities
522 (Rivero and Casas 1999; Olson et al. 2000; Jervis et al. 2008). In addition, body size,
523 generally reflects the putative energetic reservoirs. Indeed, the egg maturation, either
524 when nutrition is provided or not, is higher in largest *M. rudibundus* females respect to
525 smallest ones (Bezemer et al. 2005). In contrast to general patterns, maturation rates are
526 not correlated with size in *Trichogramma nubilale* Ertle & Davis (Hymenoptera:
527 Trichogrammatidae), thus implying that size-related differences are attributable to first
528 day's egg load rather than to maturation rate in this species (Olson and Andow 1998).
529 Unlike previous reports, adult females of the solitary koinobiont *I. leucospoides* do not
530 increase their post-emergence egg maturation according to food supply. However, this
531 synovigenic species shows a high ovigeny index (the ratio between the initial egg load
532 and the potential lifetime fecundity), which is more similar to those of proovigenic
533 species respect to synovigenic, thus adult feeding has not effect on egg production
534 (Fischbein et al. 2013).

535 Usually, the rate of egg resorption is higher for starved wasps (Jervis and Kidd
536 1986; Antolin and Williams 1989; Heimpel et al. 1997; Stokkebo and Hardy 2000),
537 since females generally increase life expectancy and the eventuality of find suitable
538 food sources (Collier 1995; Heimpel et al. 1997). Several parasitoids species can resorb
539 eggs to improve their lifespan when exposed to water diet (Heimpel et al. 1997; Lee and
540 Heimpel 2008b; Richard and Casas 2009). Nevertheless, when egg resorption is not
541 allowed or does not considerably raises life expectancy, the increasing of egg
542 maturation by starved wasps may be an advantageous adaptive strategy to improve the
543 lifetime fecundity (Roitberg et al. 1992; Fletcher et al. 1994). For instance, starved
544 *Macrocentrus cingulum (=grandii)* Brischke (Hymenoptera: Braconidae) females have

545 a significant higher number of egg load respect to sugar-fed ones, since they no
546 evidence egg resorption, which is recorded for well-fed wasps (Olson et al. 2000).
547 Similarly, during the early adult life of the braconid *Microplitis rufiventris* Kokujev,
548 potential fecundity seems subjected to feeding status, since higher rates of egg
549 maturation are related to starved wasps, which potentially compensate shorter life
550 (Hegazi et al. 2013). In contrast, when lacking both suitable food and host, starved
551 females may invest their residual energy in locomotion to find a more profitable
552 microhabitat.

553 Host hemolymph absorbed through host feeding may also play a pivotal role in
554 egg maturation, usually increasing egg maturation rate and deterring egg resorption. The
555 synovigenic *O. nezarae* is a concurrent host feeder, usually exploiting this nutritional
556 source before oviposit. Females emerge with no mature eggs, but they mature two eggs
557 after a single host feeding (Aung et al. 2012). Furthermore, host feeding is not crucial
558 but helpful to enhance egg maturation in *A. melinus, Metaphycus flavus* Howard and *M.*
559 *luteolus* Timberlake, since the host meal contributes to egg maturation just when
560 coupled with honey supplement (Heimpel et al. 1997, Kapranas and Luck 2008). Some
561 amino acids and minerals readily available in host hemolymph are found to be essential
562 for egg maturation in an ichneumonid parasitoid (Bracken 1965), whereas protein
563 supplementation seems to have no impact on trichogrammatid species (Ashley and
564 Gonzalez 1974). Also Giron et al. (2004) investigated the effect of a single host-meal on
565 parasitic wasp egg production. Females of *E. vuilletti* obtained energy to produce just
566 1.53 eggs per host meal, due to the low lipid content of hemolymph (Giron et al. 2004).
567 Conversely, the strong synovigenic parasitoid *D. isaea* improves its potential fecundity
568 respect to water supply and increase the lipid level when it feeds on hosts, highlighting

569 the presence of a lipogenesis pathway (Zhang et al. 2011), which is absent in other
570 species (Olson et al. 2000). Among lipids, poly-unsaturated fatty acids (PUFA) are
571 known to be suitable for energetic purposes, but most insect are unable to synthesize
572 long-chain lipids (Visser et al. 2010). As reported for carbohydrates, different fatty acids
573 may influence differently on parasitoid life-history traits. *P. turionellae* produces eggs
574 differentially in response to several fatty acid free diets. While the absence of single
575 fatty acid (palmitic, stearic, oleic and linolenic acid) does not influence the egg loads in
576 comparison to fatty acid-rich or natural diets, fatty acid-free and linoleic acid-free diets
577 dramatically decrease the potential fecundity (Nurullahoglu and Ergin 2009). The
578 crucial importance of linoleic acid may be attributed to its role as structural component
579 of membranes and as precursor of eicosanoids, which act as oviposition stimulants
580 (Stanley-Samuelson 1994). Furthermore, host feeding is generally crucial for amino
581 acid intakes. However, the addition of synthetic amino acids or host hemolymph to
582 honey diets does not increase oogenesis in inexperienced *C. grandis*, whereas females
583 with ovipositional experience increase their egg maturation rate when fed on the
584 supplemented diet (Morales-Ramos et al. 1996). Furthermore, host-food does not
585 prevent egg resorption in absence of a supplemental food source (Heimpel et al. 1997),
586 even if it seems fundamental to prevent this phenomenon in the eulophid species
587 *Tamarixia radiata* (Waterston) (Chen and Stansly 2014).
588 Generalist species, which usually feed in highly variable microhabitats, are
589 typically more flexible and adaptable to nutrient and host deficiency than specialist
590 species. Cicero et al. (2012) investigated the effect of different diets, including hosts of
591 different quality, on four braconid species: *D. longicaudata*, *Doryctobracon crawfordi*
592 (Viereck), *Utetes anastrephae* (Viereck) and *Opius hirtus* (Fisher). Whereas the

593 generalist *D. longicaudata* increases its egg load and maturation rate when feeds on
594 different quality hosts, the specialist *O. hirtus* increases its egg load only when feeds on
595 low quality hosts (Cicero et al. 2012).
596 Lastly, the potential fecundity can also be influenced by food provisioning in
597 dipteran parasitoids. Feeding on raisins greatly increases the number of egg produced by
598 *T. giacomellii* females, respect to water-fed insects, although no effect is detectable on
599 number of ovarioles and body size (Coombs 1997).
600
601 ***Fecundity, fertility and parasitism***
602
603 Here the effects of diet composition and frequency on (*i*) parasitism behavior
604 (i.e. number of oviposition or eggs laid), (*ii*) fertility (i.e. the natural ability to produce
605 offspring) (*iii*) and daily and lifetime fecundity (i.e. the actual reproductive rate) of
606 parasitic wasps are reviewed.
607 Natural or artificial diets can alter the oviposition behavior of parasitoids,
608 modifying either the propensity to oviposit or the number of egg laid. Overall, the
609 supply of optimal sugar-rich diet to parasitoid female increases the oviposition behavior.
610 The effect of nectar, honeydew, hosts and artificial diets on parasitism of the
611 proovigenic parasitoid *Copidosoma koehleri* Blanchard (Hymenoptera: Encyrtidae) was
612 investigated by Baggen and Gurr (1998). While host presence does not influence
613 parasitization rate, supplemental nutrition of honey or suitable nectar plants nearly
614 doubles the oviposition behaviors of *C. koahleri* females (Baggen and Gurr 1998).
615 Honey-based diet and sucrose syrup-based ones are reported as the best options to
616 increase parasitization rates in *Trichogramma euproctidis* (Girault) (Hymenoptera:

617 Trichogrammatidae), probably due to the high suitability of this sugary source coupled
618 to a quick access to food (Tunçbilek et al. 2012). Similarly, *O. nezarae* lays more eggs
619 in presence of honey, suitable flower nectar or sugar (glucose, galactose and sucrose)
620 nutrition, if compared to aphid honeydew (Teraoka and Numata 2000). Nevertheless,
621 the exposure to hosts coupled with sugar or honey food increase parasitization rates in
622 *C. plutellae*, whereas the total absence of supplemental food does not enhance
623 oviposition behavior neither in presence of high host-density scenarios (Mitsunaga et al.
624 2004). Food deprivation affects also the ratio between host feeding and parasitism in the
625 aphelinids *E. melanoscutus* and *E. formosa*. In both species, food-deprived wasps killed
626 more hosts by feeding, while fed females had greater parasitization rates (Zang and Liu
627 2010). Similarly, also the eulophid parasitoid *N. formosa* benefits from honey
628 supplement by reducing the host-feeding events in favor of oviposition, increasing also
629 the total host mortality (Liu et al. 2015). Oviposition behavior may also be deterred by
630 the direct exposure to food contaminants, such as lectins, reducing the number of total
631 egg laid by the parasitoid *E. pennicornis* (Wakefield et al. 2010).
632 The presence of optimal food sources is considered helpful to improve parasitoid
633 fertility and fecundity. Fertility of braconid parasitoid *O. hirtus* is improved when
634 females feed on sugar-rich artificial diets (Cicero et al. 2012), whereas the
635 administration of aphid honeydew to *T. ostriniae* females showed no effect on fertility
636 of egg laid, even if the parasitization rate were higher (Fuchsberg et al. 2007). Host
637 feeding strategy is also important to improve lipid levels and consequently egg fertility
638 (Zhang et al. 2011) in those species that are able to exploit a lipidic nutrition during
639 adulthood (Visser et al. 2010). Indeed, the presence of fatty acid in the diets
640 administrated to *P. turionellae* wasps is strictly related to higher egg fertility and

641 hatching percentage (Nurullahoglu and Ergin 2009).

642 Fecundity and progeny production are heavily affected by diet composition,
643 either by directly improving female reproductive mechanisms, as well as by prolonging
644 adult lifespan and consequently parasitoid lifetime fecundity. In several mymarid and
645 braconid parasitoids, the lifetime fecundity increases when reared on honey diet, mainly
646 boosting daily fecundity (Jacob et al. 2006; Wu et al. 2008; Mutitu et al. 2013).
647 Furthermore, the fecundity of *F. arisanus* is high when fed on honey, molasses, maple
648 syrup and sugar cane, but daily fecundity varies accordingly to quality of diet (Bautista
649 et al. 2001). Similarly, Tena et al. (2013b) compared the effect of five kinds of
650 honeydew on the realized fecundity of *A. melinus*. The realized fecundity of females
651 with access to low-value food, as the honeydew excreted by the aphid *Aphis spiraecola*
652 Patch (Aphididae), was similar to unfed females. In contrast, females fed on honeydew
653 of *Coccus hesperidum* L. (Coccidae) and *Icerya purchasi* Maskell (Monphlebidae),
654 which contain high nutritional valuable carbohydrates, had a realized fecundity six
655 times greater (Tena et al. 2013b). Even pollen may be exploited as food source to
656 improve fecundity. *T. brassicae* wasps increase their lifetime fecundity when fed with
657 pollen and water mixture respect to water-fed females, but since pollen is a sub-optimal
658 food source, the addition of honey or the supply of honey solution determine greater
659 positive effects on progeny production (Zhang et al. 2004). Low-quality diets can also
660 lack impact on fecundity of females, with similar results to starved ones. Schmale et al.
661 (2001) reported no differences in fecundity for the pteromalid parasitoids *D. basalis* and
662 *A. calandrae*, as well as for the braconid *H. prosopidis*, three putative hymenopteran
663 parasitoids of *Acanthoscelides obtectus* (Say) (Coleoptera: Bruchidae) when fed on
664 sugarcane or without food supplements. On contrast, for all three tested species, females

665 produced more offspring when provided with a honey-based diet (Schmale et al., 2001).
666 Although different nutritional sources generally alter parasitoid fecundity, this is not the
667 case of the encyrtid *A. papayae*, which can equally benefit from honey solution, as well
668 as from honey and yeast extract diet, dried grapes extract and fructose solution (Divya
669 et al. 2011). Frequency of feeding may also play a role on wasps' fecundity. Indeed, *C.*
670 *marginiventris* females produce more offspring when sugar-rich nutrition is
671 continuously provided (Faria et al. 2008). Similarly, when fed *ad libitum*, *M.*
672 *pulchricornis* females produced significantly more progeny than those subjected to
673 lower feeding frequencies, increasing daily fecundity rather than extending their
674 reproductive period (Wu et al. 2008).
675 Food supply may evoke different effect on daily offspring production and on
676 duration of the reproductive period. *D. basalis* and *H. prosopidis* shows higher daily
677 fecundity when allowed to feed on honey, respect to sugarcane, but no differences are
678 recorded after 25 day on cumulative progeny production of *D. basalis* (Schmale et al.
679 2001). Similar results are described for *M. rufiventris* wasps, since starved females lay
680 more eggs than do honey-fed ones in the first day after emergence, probably as
681 consequence of exclusive energy allocation for reproductive activities (Hegazi et al.
682 2013). The impact of nutrition on lifetime fecundity depends also on the interaction with
683 parasitoid physiology, mostly size and age. For example, the realized lifetime fecundity
684 of *T. nubilale* varies according to the wasp's size, and the honey impact on fecundity is
685 higher for small females, while no differences are reported for unfed wasps (Olson and
686 Andow 1998). Parasitoid age plays a pivotal role for *P. cerealellae* wasps, which behave
687 differently to various diet accordingly to age. Whereas the young females are not
688 immediately conditioned by different diet composition or even by the absence of food,

689 the older females benefit from sugar feeding, increasing lifetime fecundity (Onagbola et
690 al. 2007).
691
692 ***Sex ratio***
693
694 Several parasitic wasps are able to adaptively control sex ratios, selecting
695 offspring sex ratio in response to various factors, mainly represented by local mate
696 competition and by host quality (Godfray and Werren 1996). Commonly, well-fed
697 female parasitoids alter the progeny sex ratio producing a higher proportion of female
698 offspring. Accordingly to Berndt and Wratten (2005), in absence of flower nectaries, *D.*
699 *tasmanica* sex ratio is strongly male biased, but, when wasps feed on flowers,
700 approximately an equal sex ratio was produced , with exclusive male production at the
701 end of female's life. The diet of adult parasitoids is unlikely to affect inbreeding,
702 superparasitism and host size, while it could play a role in mating success, sperm
703 viability or fertilization, which may explain sex ratio variation. Well-fed
704 *Pachycrepoideus vindemmiae* (Rondani) females also exploit nutrition by producing a
705 higher proportion of female offspring (Hu et al. 2012). In absence of honey, progeny sex
706 ratio is always female biased but with an increase of male percentage, while total
707 progeny production is significantly lower (Hu et al. 2012). Furthermore, also *T.*
708 *ostriniae* produces a higher proportion of females and a greater daily fecundity when
709 parasitoids were fed with aphid honeydew compared to unfed wasps (Fuchsberg et al.
710 2007). Similarly, honeydew feeding increases the total progeny and the relative number
711 of females in *Lipolexis scutellaris* Mackauer (Hymenoptera: Braconidae) (Singh et al.
712 2000). Conversely, the solitary egg parasitoid *C. noackae,* if allowed to fed on sugary-

713 rich diet, produces a slightly male-biased progeny sex ratio, in contrast to the female-
714 based offspring produced when females are starved (Mutitu et al. 2013). Moreover, *A.*
715 *papayae* sex ratio is not influenced by the presence or the kind of food sources,
716 although the fecundity is increased (Divya et al. 2011).
717
718 **Conclusions and implications for biological control and IPM**
719
720 A prerequisite for parasitoid effectiveness against pests in the field is nectar
721 and/or honeydew accessibility, which typically enhance survival, dispersal and fertility
722 (Wäckers et al 2008). Nevertheless, modern agriculture had led to agro-ecosystem
723 landscape simplification, which contributes to an increase in pest density and to a
724 reduction to alternative non-crop food sources available for natural enemies. Moreover,
725 the commuting behavior (i.e. the return of a parasitoid to the original host location, after
726 feeding elsewhere) (Jervis et al. 1993) is still poorly understood and, apart from the
727 energetic costs and predatory risk, longer distances between food and host locations and
728 the presence of alternative hosts may make commuting less profitable for parasitoids,
729 decreasing host fidelity.
730 In this scenario, a better understanding of parasitoid feeding ecology is needed to
731 identify suitable food sources in the field. Besides the well-known HPLC-sugar analysis
732 of food sources available in the agro-ecosystems, molecular approaches may be helpful
733 to identify both plant and animal-borne foods suitable for adult parasitoids (reviewed by
734 Traugott et al. 2013). DNA-based techniques (i.e. next-generation sequencing and
735 multiplex PCR) may be employed to investigate which kind of food is used by
736 parasitoid in field, while stable isotope and fatty acids may be helpful to examine the

737 differential assimilation and metabolism of a broad range of food sources, highlighting
738 the nutrient and energy fluxes in the food web and the presence of nutrient limitations.
739 Indeed, for parasitoids the presence of adequate sugary sources is fundamental to ensure
740 appropriate host parasitization rates. Segoli and Rosenheim (2013) reported that
741 *Anagrus* parasitoids in unsprayed vineyards survive less than a day and the proportion
742 of fed wasps is generally really low (about 10% on average). In addition, seasonal
743 changes in nutrient availability and quality may also play a key role in parasitoid
744 efficiency, as reported for *A. melinus*, which could be limited by honeydew paucity and
745 accordingly could reduce its potential as biological control agents (Tena et al. 2013a).
746 To overcome occurred field limitations, the employment of artificial sugar
747 sources, flowering cover crops and the management of flowering field margins may be
748 helpful to improve natural populations and to enhance the performance of parasitic
749 wasps in both conservative and augmentative biological control programs. Indeed, since
750 crops usually provide nectar for a limited period, commonly the only source of non-host
751 food are wildflowers, including weeds (Altieri et al. 1977; Rollin et al. 2016), and
752 honeydew (Tena et al. 2016). However, plant nectar and honeydew are not always
753 profitable for parasitoids, since accessibility, quantity, quality and detectability of
754 resources may be weak (Bianchi and Wäckers 2008; Tena et al. 2013a, b; Tena et al.
755 2016). Many parasitoid species exploit nectars from various cover crops and field
756 margins' plants differently, accordingly to sugar composition and content (Vattala et al.
757 2006), and accessibility of nectars (Idris and Grafius 1995; Baggen and Gurr 1998).
758 Thus, the mere presence of flowering weeds or cover crops does not ensure food
759 accessibility for parasitoids (Lee et al. 2006), since a great number of natural occurred
760 plants are or not attractive or even repellent for them (Heimpel and Jervis 2005;

761 Wäckers 2004). On this basis, intercrop plant varieties, with an increased number of
762 nectaries, as well as with an extended nectar production period (Rollin et al. 2016), can
763 highly benefit parasitoids, by providing high quality food and influencing various life
764 traits (Jamont et al. 2013).

765 In the case of honeydew, its exploitation by parasitoids depends greatly on its
766 quality. Therefore, it is essential to test the quality of the honeydew for parasitoids to
767 determine whether this sugar source can increase parasitoid fitness (Tena et al. 2013b;
768 Tena et al. 2016).

769 Furthermore, additional energy may be obtained by artificial sugar
770 supplementation, as reported for *A. melinus* in field (Tena et al. 2015). Commercial food
771 spray (Eliminade) has been proved to expand survival of some parasitoid species, but
772 also among closely related species variations of nutrition benefits could be recorded
773 (Irvin et al. 2007), while proteic supplement was not effective (Wade et al. 2008a).
774 Nevertheless, the use of artificial sugar spray and food supplementation has not proven
775 effective in many agroecosystems (Wade et al. 2008b). Since food is not always limiting
776 in field, food supplements need to be appropriate and the nutrients suitable to enhance
777 not only parasitoid longevity and fitness, but also their parasitization ability under field
778 conditions (Sigsgaard et al. 2013). Concerning sugar-spray food, limited information
779 has been provided for the effectiveness of other feeding devices containing mixture of
780 honey and/or carbohydrates, mainly used in greenhouse crop systems (Shimoda et al.
781 2014). In some tri-trophic microhabitats, pest and parasitoid food resources are the
782 same, and to control herbivorous populations various insecticidal-bait formulation
783 containing food attractants are used. In this context, baits may also attract non-target
784 species, as parasitoids, which may be killed by insecticides, but also may indirectly alter

785 their foraging behavior in presence of a competitive food source (Wang et al. 2011).

786 The major challenge, however, is the selection of plant species and/or artificial
787 sugars that encourage beneficial arthropods but not the pest. Indeed, it has been reported
788 that flowering plants exploited by hymenopteran parasitoids are also an appropriate
789 food source for their lepidopteran pests, although nectar has a much greater effect on
790 parasitoid longevity than on herbivores (Winkler et al. 2009). However, peculiar
791 carbohydrates present in hemipteran hemolymphs (i.e. trehalose) are not beneficial for
792 herbivores and could be applied as selective food source (Winkler et al. 2005).
793 Moreover, beside the majority of research being focused on selectivity of food
794 supplementation in a specific tri-tropic interaction (Begum et al. 2006), little attention
795 has been given to the effect of sugar supplement toward non-target pests, which could
796 benefit from additional food provisioning and make decrease crop yields (Mitsunaga et
797 al. 2006). Furthermore, also hyperparasitoids may exploit supplemental nutrition,
798 including honeydew saccharides that are not profitable for herbivorous pests, and this
799 can boost their longevity and double their fecundity (Harvey et al. 2012). Even if
800 hyperparasitoids lead to herbivore death, a large presence of these arthropods can cause
801 the failure of a biological control program by dramatically decreasing parasitoid
802 populations.

803 Finally, implementation of food sources under field condition, via artificial diet
804 provisioning or flowering plant management, has to consider the innate preferences of
805 parasitoids. Alternatively, also the ability to learn peculiar odor in association with
806 sugary diets may be helpful to prime parasitoid responses during mass rearing or to
807 increase food fidelity in field. Beside direct field application of food supplements,
808 knowledge about diet influence on parasitoid life-history traits is essential to improve

809 mass-rearing techniques of biocontrol agents employed in inundative and
810 augumentative programs. Prior the field release, it seems therefore advisable to supply
811 insects with sugar-rich diets and host food to improve their performances in fields and
812 to optimize parasitoid egg expenditure (Hougardy et al. 2005; Hougardy and Mills
813 2006, 2007). Furthermore, little research on the effects of the adult diet on parasitoid
814 courtship and mating traits has been conducted. Further studies on this issue, as well as
815 on the employment of food sources as effective baits for parasitoid monitoring (Li et al.
816 2015) are urgently needed to maximize the field effectiveness of these biological control
817 agents.
818
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820
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